

An Ethogram of the Toad-headed Lizard *Phrynocephalus vlangalii* during the Breeding Season

Yin QI¹, Shasha LI², Langduoerji SUO³, Hua LI³ and Yuezhaio WANG^{1*}

¹ Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, Sichuan, China

² College of Life Sciences, Sichuan University, Chengdu 610041, Sichuan, China

³ Management Bureau of Zoige Wetland Nature Reserve, Aba 624500, Sichuan, China

Abstract In this study, we intended to construct an ethogram of the toad-headed lizard *Phrynocephalus vlangalii* by classifying and describing its behaviors using the Posture-act-environment (PAE) method. Through direct field observation and video recording, we obtained eight postures, sixty-two acts and ten environments, and thus we formed an ethogram consisting of eighty-three behaviors encoded with PAE. A complete ethogram for a species could provide systematic behavioral information which helps to understand the connections among related behaviors and provides background information for specific behavioral study, hence the present ethogram will be greatly useful for future behavioral studies on *P. vlangalii* as well as other *Phrynocephalus* species.

Keywords reproductive behavior, *Phrynocephalus vlangalii*, PAE coding, posture-act-environment, tail curling

1. Introduction

Describing and classifying the behaviors of a species, thereby forming an ethogram, is the first step in studying the behavior for a particular species (Martin and Bateson, 2007). In general, an ethogram can reveal behavioral information for a species' entire life history or a particular life stage, thus, be extremely helpful for the formulation of new questions and hypotheses (Jenssen, 1971; Greenberg, 1977; Torr and Shine, 1994; Hanlon *et al.*, 1999; Li *et al.*, 2001; Zeng *et al.*, 2001; Langkilde *et al.*, 2003; Pandav *et al.*, 2007). One issue with previously published ethograms is the variability in behavioral conditions (many ethograms were established based on behavioral records from laboratory conditions, which may not accurately reflect the behaviors of a species in its natural setting; Nunes *et al.*, 2009) and descriptive methodology. Pertaining to the latter concern, the Posture-act-environment (PAE) method has been increasingly suggested to be used in ethogram construction due to its highly informative and robust method for coding animal behaviors (Jiang, 2000). In the PAE coding system, posture reflects the shape and

spatial location of an individual's specific body structure within a time period; act describes the movements of the individual's specific body parts, and environment reflects the biotic or abiotic environment within which the behaviors occur. In previous studies, different behaviors described by the PAE coding system were classified according to their behavioral consequences (Jiang, 2000; Jiang *et al.*, 2001; Long *et al.*, 2008).

Ethograms are available for some commonly studied species, especially for some endangered species in China, such as the Père David's Deer (*Elaphurus davidianus*, Jiang, 2000; Li *et al.*, 2001), Dwarf Blue Sheep (*Pseudois schaeferi*, Long *et al.*, 2008), Hainan Eld's deer (*Cervus eldi hainanus*, Zeng *et al.*, 2001; Liu *et al.*, 2007) and Yangtze finless porpoise (*Neophocaena phocaenoides*, Xiao and Wang, 2005). However, ethogram studies are lacking in small vertebrates, and are particularly rare for amphibians and reptiles (Liu *et al.*, 2009). Lizards are often regarded as excellent models for the study of behavioral and signal evolution due to the wide array of characteristics exhibited by distinct groups (Langkilde *et al.*, 2003). Some species within the squamate families Iguanidae, Agamidae, and Scincidae are being increasingly studied due to their display behaviors and specialized morphological characters. However, the published ethograms on lizards only focus on some American and Australian species (Carpenter, 1967; Jenssen, 1971; Torr

* Corresponding author: Prof. Yuezhaio WANG, from Chengdu Institute of Biology, Chinese Academy of Sciences, with his research mainly focusing on phylogeny and ecology of reptiles.

E-mail: arcib@cib.ac.cn

Received: 13 May 2011 Accepted: 21 June 2011

and Shine, 1994; Zhao, 1999; Langkilde *et al.*, 2003). To our knowledge, at present, no ethogram on lizards from China has been reported.

In this study, we describe and classify the behaviors of the toad-headed lizard (*Phrynocephalus vlangalii*) throughout its breeding season by using the PAE method. This lizard is an alpine desert species which is ovoviviparous, and distributed at an elevation from 2000 m to 4500 m (Zhao, 1999). Previous studies on its morphology and display behaviors all suggested that *P. vlangalii* is particularly well suited for signal evolution study (Zhao, 1999; Qi *et al.*, 2011). Thus, the establishment of an ethogram for *P. vlangalii* under natural conditions is of great importance to the behavioral studies of this species in the future.

2. Materials and Methods

2.1 Study area Field work was conducted during the reproductive period of *P. vlangalii* from May to June in 2009 in an area close to the Xiaman, Zoige (Ruoergai) Wetland Nature Reserve in Sichuan, southwestern China (33°43'25" N, 102°29'04" E; elevation 3464 m). In this area, *P. vlangalii* populations can be found in the sparsely vegetated sand dunes, which are surrounded by wetland (Figures 1, 2). The vegetation on and around these sand dunes is predominantly composed of three grass species (*Kobresia humilis*, *K. prattii* and *Elymus natans*) and a shrub (*Salix sclerophylla*).



Figure 1 *Phrynocephalus vlangalii* in its habitat

2.2 Enclosures and captures According to the method of Aragon *et al.* (2004), a 50 m × 40 m plot was set up and divided into twenty 10 m × 10 m quadrats, to form a grid in the field. This plot provided a relatively stable observation platform for our study. All animals observed in the plot were caught by noosing or pitfall traps. Immediately after capturing a lizard, we marked it by toe clipping



Figure 2 Habitat of *P. vlangalii* close to the Zoige Wetland Nature Reserve in Sichuan, China

and each was given a unique color code on its dorsum using acrylic paint. The paint allowed us to monitor it from a distance of more than 4 m with the aid of 10 × 35 binoculars without disturbing the animal's natural behaviors. Toe clipping was used for permanent marking because this method has been shown to have no effect on lizard behaviors or fitness in other species (Morrison *et al.*, 2002). All captured lizards (45 males, 76 females) were released back to their capture sites within 5 min. Sexual maturity of each lizard was estimated from its SVL (> 51 mm for adult males and females) (Wu *et al.*, 2002). Males were distinguished from females by hemi-penal bulges.

2.3 Observation and behavioral coding A combination of focal (focusing on an individual lizard) and behavioral sampling (focusing on specific behavior) was used to monitor lizard activities. Two periods of time were chosen to conduct our censuses each day, in the morning (0900–1230 hours) and in the afternoon (1230–1630), respectively. During each census, we searched for marked lizards at random with the aid of 10 × 35 binoculars, and if the lizard remained undisturbed, a JVC GZ-MG 157 micro-camera was used to record its behaviors for at least 10 min as the focal lizard moved throughout the environment. Sampling was conducted for at least 10 min, following the protocols of previous studies on display behaviors of lizards in the field (Perry *et al.*, 2004; McElroy *et al.*, 2007). During the behavioral observation, we tried to minimize the disturbance to the focal lizard by maintaining a distance of >5 m. A maximum of two sightings for each individual were scored per day. Field work conducted exclusively on sunny days with air temperatures ranging from 20 °C to 26 °C. In the lab, forty-three behavioral videos (15 hours) from 29 individuals (15 males, 10 females and 4 juveniles) were scored and divided into discrete categories according to

the PAE coding method suggested by Jiang (2000).

3. Results

Eight kinds of postures were discriminated and coded as P-code elements according to the shape and spatial location of an individual's main body structure within the time period. These included: standing, crouching, rearing, sitting, lying, rolling, walking and running (see Table 1). The eight postures occurred in both males and females. Generally, standing, crouching, rearing, sitting and lying are static postures, while rolling, walking and running are dynamic postures. Standing is defined as four limbs extended vertically and perpendicular to the anterior-posterior axis and held against the body; crouching is defined as forelimbs extended with hindlimbs bending and held against the body; rearing is defined as standing on both hindlimbs, forelimbs pressing against plant, and the whole body in upright position; lying is defined as the backside flattening onto the substrate; rolling is defined as whole body rolling laterally; walking is defined as four limbs moving in a staggered sequence and propelling the body forward; and running is defined as four limbs moving in a staggered sequence quickly and propelling the body forward.

Sixty-two acts were discriminated and coded as A-code elements according to a lizard's movement of specific body parts, such as mouth, head and neck, eyes, limbs, hindquarter, chest and belly, and tail (see Table 2). At the same time, we summarized the environmental elements (or conditions) under which different behaviors occurred as E-code elements (see Table 3).

Eighty-three behaviors were discriminated and described by PAE-coding and grouped into nine categories according to their behavioral functions. These include: courting, mating, parturition, territoriality, display, ingestion, waste elimination, resting and thermo-regulation, and locomotion (see Table 4).

4. Discussion

4.1 Function of ethogram Establishment of an ethogram is very important for behavioral studies (Jiang, 2001; Martin and Bateson, 2007). Before detailed studies of specific behaviors are able to be conducted, we need a comprehensive knowledge of the basic behavior patterns exhibited by a species. A complete ethogram for a species could provide systematic behavioral information which helps to understand the connections among related behaviors and provides background information

Table 1 Posture codes for the toad-headed lizard *P. vlanguilii* in breeding season

Posture	Code
Standing	1
Crouching	2
Rearing	3
Sitting	4
Lying	5
Rolling	6
Walking	7
Running	8

for specific behavioral function, evolution, and development (Barnard, 2004). In addition, the ethogram can also facilitate behavioral measurement, sorting and analysis (Ottoni, 2000; Long *et al.*, 2008). PAE methodology allows for the recording of focal behaviors according to PAE coding to classify behaviors, and then analyze each behavioral element separately. We were then able to choose the proper recording method based on the characters of different behavioral elements. For example, time sampling is suggested to be suitable for the recording of acts, whereas instantaneous sampling may be more suitable for the recording of postures (Orrell and Jenssen, 2003; Bloch and Irschick, 2006; Martin and Bateson, 2007).

4.2 Courting behaviors The ethogram of the toad-headed lizard shows that the courting behaviors have different modes among individuals. This phenomenon has been documented in the studies on other animals (see Dominey, 1984; Shine *et al.*, 2005). The courting behaviors of male toad-headed lizards vary enormously. For example, some males approach and attack focal females directly and forcefully, even invading female burrows, while other males approach focal females slowly accompanied with a tail display. The most interesting behaviors observed were that some males either hide themselves near females' burrow with their four limbs and body flattened on substrate, to wait for the females' appearance from the burrows, or defend the females to prevent sneaking by other males (Table 4). Those different courting modes might represent alternative mating tactics, but this speculation needs more empirical support (Dominey, 1984; Zeng *et al.*, 2001; Li *et al.*, 2001). No matter what kind of courting mode exhibited, intense combat between males and females occurs before mating. There are several hypotheses associated with the function of fighting between males and females: 1) male fighting is a coercive mating tactic (Clutton-brock and Parker, 1995); 2) male

Table 2 Act codes for the toad-headed lizard *P. vlangalii* in breeding season

Act	Code	Act	Code
Mouth			
Closing mouth	1	Forelegs bending forwards	32
Opening mouth	2	Hindlegs bending backwards	33
Chewing	3	Hindquarter	
Biting	4	Back straightening	34
Showing teeth	5	Back arching	35
Swallowing	6	Tail base arching	36
Head and Neck		Trunk compressing	37
Raising head	7	Left bending	38
Lowering head	8	Right bending	39
Shaking	9	Lying	40
Extending forward	10	Defecating	41
Turning left	11	Urinating	42
Turning right	12	Thrusting	43
Swaging	13	Erecting	44
Rubbing	14	Inserting	45
Turning back	15	Giving birth	46
Eye		Chest and Belly	
Closing eyes	16	Arching	47
Staring while in social conflict	17	Clinging	48
Glancing	18	Flattening	49
Watching	19	Rubbing	50
Limbs		Thrusting	51
Pawing	20	Tail	
Holding	21	Tail straightening	52
Standing	22	Tail parallel bending	53
Running	23	Tail-tip vertically curving	54
Forelegs straightening	24	Tail vertically curving	55
Forelegs bending	25	Tail wagging	56
Standing with forelegs apart	26	Tail supporting	57
Hindlegs straightening	27	Tail-base supporting	58
Hindlegs bending	28	Tail flapping	59
Standing with hindlegs apart	29	Tail turning down	60
Forelegs standing in upright	30	Rubbing	61
Hindlegs pressing against plants	31	Shaking	62

Table 3 Environment codes for the toad-headed lizard *P. vlangalii* in breeding season

Environment	Biotic	Abiotic	Code
Sand		√	1
Shrub		√	2
Burrow		√	3
Single	√		4
Male	√		5
Female	√		6
Juvenile	√		7
Insect	√		8
Predator	√		9
Mixed gender	√		10

fighting stimulates females to reach sexual synchrony (personal communication with Prof. Haitao SHI); and 3) female fighting is a cryptic pattern of mate choice (Andersson, 1994). Verification for the above assumptions needs further research.

4.3 Tail display The ethogram shows that tail displays (curling, wagging and shaking) of the toad-headed lizards may function during courting behavior, territorial behavior and foraging behavior. Regardless of the courting mode, males curl or wag tails before approaching females, and females respond to males by tail curling and wagging similarly. During territorial interactions, the territory defender always signals towards the intruder by tail curling, and

Table 4 PAE codes for the behaviors of the toad-headed lizard *P. vangalii* in breeding season

Behavior	Male (15)	Female (10)	Juvenile (4)	Sequential code	PAE code		
					P	A	E
Courting behavior							
Hiding	++			1	4	25, 28, 48	1, 2 ,3, 6, 10
Waiting while standing	++			2	1	11, 12, 19, 24, 27	1, 2, 3, 6, 10
Waiting while crouching	++			3	2	11, 12, 19, 24, 28	1, 2, 3, 6, 10
Waiting while rearing	+			4	3	11, 12, 19, 27, 30	1, 2, 3, 6, 10
Waiting while sitting	++			5	4	18, 25, 28, 48	1, 2, 3, 6, 10
Alluring while standing	++			6	1	24, 27, 54, 55, 56	1, 2, 3, 6, 10
Alluring while crouching	++			7	2	24, 28, 54, 55, 56	1, 2, 3, 6, 10
Approaching	++	+	+	8	7	9, 24, 27, 55, 56	1, 2, 3, 4, 5, 6
Intruding into burrow	+			9	7	24, 27, 37	3
Fighting	++			10	1	2, 4, 10, 24, 35, 37, 47, 55, 56	1, 2, 3, 6, 10
Guarding while standing	+			11	1	24, 27, 54, 55, 56	1, 2, 3, 6, 10
Guarding while crouching	+			12	2	24, 28, 54, 55, 56	1, 2, 3, 6, 10
Departing	++	+	+	13	7	9, 25, 28, 55, 56	1, 2, 3, 4, 5, 6
Mating behavior							
Fighting	++	++		14	1,7,8	2, 4, 10, 24, 35, 37, 47, 55, 56	1, 6
Conquering	++	+		15	1	21	1, 6
Resistwing	+	++		16	1,5,6	21, 62	1, 6
Controlling	+	+		17	5,6	21, 54, 55	1, 6
Wallowing	+	+		18	6	21	1, 6
Coercive mating	+	+		19	1,5	44, 51	1, 6
Post-copulatory stance	+			20	1,2	24, 28, 34, 52	1, 6
Parturition behavior							
Pre-parturition stillness		++		21	1	24, 27, 34	1, 2, 3, 4, 10
Parturition		++		22	1	26, 29, 34, 46	1, 2, 3, 4, 10
Moving slowly		++		23	7	26, 29, 34	1, 2, 3, 4, 10
Post-parturition stillness		++		24	4	26, 29, 34	1, 2, 3, 4, 10
Tail wagging		++		25	1,7	25, 28, 56	1, 2, 3, 4, 10
Territorial behavior							
Alerting while standing	++	++		26	1	11, 12, 19	1, 2, 3, 4, 5, 6, 7
Alerting while crouching	++	++		27	2	11, 12, 19	1, 2, 3, 4, 5, 6, 7, 10
Alerting while sitting	++	++		28	4	11, 12, 19	1, 2, 3, 4, 5, 6, 7, 10
Patrol	++	++		29	7	23	1, 2, 3, 4, 5, 6, 7, 10
Tail curling while standing	++	++	+	30	1	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail curling while crouching	++	++	+	31	2	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail curling while sitting	++	++	+	32	4	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail curling while moving	++	++	+	33	7	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail wagging while standing	++	++	+	34	1	56	1, 2, 3, 5, 6, 10
Tail wagging while crouching	++	++	+	35	2	56	1, 2, 3, 5, 6, 10
Tail wagging while sitting	++	++	+	36	4	56	1, 2, 3, 5, 6, 10
Tail wagging while moving	++	++	+	37	7	56	1, 2, 3, 5, 6, 10
Tail shaking	++	++	+	38	1,7	59, 62	1, 2, 3, 5, 6, 10
Fighting	++	++	+	39	1,7	2, 4, 10, 24, 35, 37, 47, 55, 56	1, 2, 3, 5, 6, 10
Chasing	++	++		40	1,8	23	1, 2, 3, 5, 6, 7, 8, 9, 10
Display behavior							
Tail curling while standing	++	++	+	41	1	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail curling while crouching	++	++	+	42	2	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail curling while sitting	++	++	+	43	4	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail curling while moving	++	++	+	44	7	54, 55	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Tail wagging while standing	++	++	++	45	1	56	1, 2, 3, 5, 6, 10
Tail wagging while crouching	++	++	++	46	2	56	1, 2, 3, 5, 6, 10
Tail wagging while sitting	++	++	++	47	4	56	1, 2, 3, 5, 6, 10
Tail wagging while moving	++	++	++	48	7	56	1, 2, 3, 5, 6, 10

(Continued Table 4)

Behavior	Male (15)	Female (10)	Juvenile (4)	Sequential code	PAE code		
					P	A	E
Tail shaking while standing	++	++	++	49	1	62	1, 2, 3, 5, 6, 10
Tail shaking while crouching	+	+	+	50	2	62	1, 2, 3, 5, 6, 10
Tail shaking while sitting	+	+	+	51	4	62	1, 2, 3, 5, 6, 10
Tail shaking while moving	++	++	++	52	7	62	1, 2, 3, 5, 6, 10
Pushing-up	++	++	+	53	2	24, 28, 34	1, 2, 3, 5, 6, 8, 9, 10
Back arching	++	++	+	54	2	24,28,35,37,47	1, 2, 3, 5, 6, 7, 8, 9, 10
Head lowering	++	++	+	55	2	8	1, 2, 3, 5, 6, 10
Head extending forward	++	++	+	56	2	10	1, 2, 3, 5, 6, 10
Ingestive behavior							
Searching while standing	++	++	+	57	1	11, 12, 18, 19	2, 3, 4, 5, 6, 7, 8, 9, 10
Searching while crouching	++	++	+	58	2	11, 12, 18, 19	2, 3, 4, 5, 6, 7, 8, 9, 10
Searching while rearing	++	++	+	59	3	11, 12, 18, 19	2, 3, 4, 5, 6, 7, 8, 9, 10
Searching while sitting	++	++	+	60	4	11, 12, 18, 19	2, 3, 4, 5, 6, 7, 8, 9, 10
Searching while moving	++	++	+	61	7,8	23	2, 3, 4, 5, 6, 7, 8, 9, 10
Feeding while standing	++	++	+	62	1	2, 3, 4, 6	2, 3, 4, 5, 6, 7, 8, 9, 10
Feeding while sitting	+	+	+	63	4	2, 3, 4, 6	2, 3, 4, 5, 6, 7, 8, 9, 10
Feeding while rearing	+	+	+	64	3	2, 3, 4, 6	2, 3, 4, 5, 6, 7, 8, 9, 10
Feeding while moving	++	++	+	65	7,8	2, 3, 4, 6	2, 3, 4, 5, 6, 7, 8, 9, 10
Swallowing	++	++	++	66	1,2,3,4	6	2, 3, 4, 5, 6, 7, 8, 9, 10
Chewing	++	++	++	67	1,2,3,4	3	2, 3, 4, 5, 6, 7, 8, 9, 10
Drinking	+	+	+	68	1	6	2
Elimination behavior							
Defecating while standing	+	+	+	69	1	8, 41, 57	1, 2, 3, 4, 5, 6, 10
Urinating while standing	+	+	+	70	1	8, 42, 57	1, 2, 3, 4, 5, 6, 10
Resting and Thermo-regulatory behavior							
Standing in bush	++	++	++	71	1	2, 22, 27, 60	2
Sitting in bush	++	++	++	72	4	32, 33, 48	2
Rearing in bush	++	++	++	73	3	27, 30	2
Standing near burrow	++	++	++	74	1	2, 7, 24, 27	3
Sitting near burrow	++	++	++	75	4	32, 33, 48	3
Crouching in sand	++	++	++	76	1	24, 28, 34	1
Sitting in sand	++	++	++	77	4	32, 33, 48	1
Rubbing in sand	+	+	+	78	4	25, 28, 48, 50	1
Locomotive behavior							
Walking	++	++	++	79	7	24, 27, 34	1, 2, 4, 5, 6, 7, 8, 9, 10
Trotting	++	++	++	80	8	23, 34	1, 2, 4, 5, 6, 7, 8, 9, 10
Galloping	++	++	+	81	8	23, 37	1, 2, 4, 5, 6, 7, 8, 9, 10
Chasing	++	++	+	82	7	10, 23, 52	1, 2, 3, 4, 5, 6, 7, 8, 9, 10
Burrow Digging	++	+	+	83	1	20, 25, 28	1, 2, 3

+ indicates that the behavior occurred at least once during video play; ++ indicates that the behavior occurred more than three times during video play

the intruder responds with tail curling or wagging. Tail displays also occur before adults or sub-adults attack their prey. Even two hour-old juvenile lizards can perform tail wagging. Similar tail displays have been found in other lizard species during social interactions, such as *Anolis carolinensis*, *Uma exsul* and *Phrynocephalus mystaceus* (Carpenter, 1967; Cooper, 1971; Zhao, 1999). Some researchers have suggested that lizards' tail displays could transmit information on their body condition and fighting capacity, so as to reduce social conflict costs (Meyers *et*

al., 2006; McElroy *et al.*, 2007), or function in sex and individual recognition (Orrell and Jenssen, 2003). Cooper (2001) suggested that the function of tail curling in the lizard *Leiocephalus carinatus* varied conditionally. It functioned as efficient deterrent to predators if lizards could escape quickly. If not, they functioned in attracting the attention of predators to their tail. To determine the function of tail displays in the toad-headed lizard, further studies are required.

Acknowledgements This work was supported by a

grant of the National Natural Science Foundation of China to Yuezhao WANG (No. 31071892). We thank Daniel NOBLE for his comments on this manuscript. We thank Yong HUANG, Hongfu WAN and Cuo KE for their assistance in the field work for this study.

References

- Andersson M. 1994. Sexual selection. Princeton, NJ: Princeton University Press, 379–395
- Aragon P., Lopez P., Martin J. 2004. The ontogeny of spatio-temporal tactics and social relationships of adult male iberian rock lizards, *Lacerta monticola*. *Ethology*, 110: 1001–1019
- Barnard C. 2004. Animal behaviour: Mechanism, development, function and evolution. Gosport, Hants: Ashford Colour Press
- Bloch N., Irschick D. J. 2006. An analysis of inter-population divergence in visual display behavior of the green anole lizard (*Anolis carolinensis*). *Ethology*, 112: 370–378
- Carpenter C. C. 1967. Display patterns of the Mexican Iguanid lizards of the genus *Uma*. *Herpetologica*, 23: 285–293
- Clutton-brock T. H., Parker G. A. 1995. Sexual coercion in animal societies. *Anim Behav*, 49: 1345–1365
- Cooper W. E. 1971. Display behavior of hatchling *Anolis carolinensis*. *Herpetologica*, 27: 498–500
- Cooper W. E. 2001. Multiple roles of tail display by the Curly-Tailed lizard *Leiocephalus carinatus*: Pursuit deterrent and deflective roles of a social signal. *Ethology*, 107: 1137–1149
- Dominey W. J. 1984. Alternative mating tactics and evolutionarily stable strategies. *Amer Zool*, 24: 385–396
- Nunes J. V., Elisei T., Sousa B. M. 2009. Outdoor enclosure to behavioral observations of lizards. *Revista Brasileira de Zoociencias*, 11: 99–101
- Greenberg N. 1977. An ethogram of the blue spiny lizard, *Sceloporus cyanogenys* (Reptilia, Lacertilia, Iguanidae). *J Herpetol*, 11: 177–195
- Hanlon R. T., Maxwell M. R., Shashar N., Loew E. R., Boyle K. L. 1999. An ethogram of body patterning behavior in the biomedically and commercially valuable squid *Loligo pealeii* off Cape Cod, Massachusetts. *Biol Bull*, 197: 49–62
- Jenssen T. A. 1971. Display analysis of *Anolis nebulosus* (Sauria, Iguanidae). *Copeia*, 2: 197–209
- Jiang Z. G., Li C. W., Peng J. J., Hu H. J. 2001. Structure, elasticity and diversity of animal behavior. *Biodiv Sci*, 9: 265–274 (In Chinese)
- Jiang Z. G. 2000. Behavior coding and ethogram of the Père david's deer. *Acta Theriol Sin*, 20: 1–12 (In Chinese)
- Langkilde T., Schwarzkopf L., Alford R. 2003. An ethogram for adult male rainbow skinks, *Carlia jarnoldae*. *Herpetol J*, 13: 141–148
- Li C. W., Jiang Z. G., Zeng Y. 2001. Bellowing, rank-class and mating success in Père David's deer stage. *Zool Res*, 22: 449–453 (In Chinese)
- Liu Y. X., Wang J., Shi H. T., Murphy R. W., Hong M. L., He B., Fong J. J., Wang J. C., Fu L. R. 2009. Ethogram of *Sacalia quadriocellata* (Reptilia: Testudines: Geoemydidae) in captivity. *J Herpetol*, 43: 318–325
- Liu Z. T., Ding J. H., Song Y. L., Zeng Z. G., Zhang Q. 2007. Wallowing behavior of Hainan Eld's deer *Cervus eldi hainanus* male during the rut and its function in reproduction. *Acta Zool Sin*, 53: 417–427 (In Chinese)
- Long S., Zhou C. Q., Wang W. K., Hu J. C., Huang Y. C., Tang L. 2008. Behavior coding and ethogram of the dwarf blue sheep. *Acta Ecol Sin*, 28: 5632–5640 (In Chinese)
- Martin P., Bateson P. 2007. Measuring Behaviour: An Introductory Guide, 3rd Edition. Cambridge: Cambridge University Press
- McElroy E. J., Marien C., Meyers J. J., Irschick D. J. 2007. Do displays send information about ornament structure and male quality in the ornate tree lizard, *Urosaurus ornatus*? *Ethology*, 113: 1113–1122
- Meyers J. J., Irschick D. J., Vanhooydonck B., Herrel A. 2006. Divergent roles for multiple sexual signals in a polygynous lizard. *Funct Ecol*, 20: 709–716
- Morrison S. F., Keogh J. S., Scott I. A. W. 2002. Molecular determination of paternity in a natural population of the multiply mated polygynous lizard *Eulamprus heatwolei*. *Mol Ecol*, 11: 535–545
- Orrell K. S., Jenssen T. A. 2003. Heterosexual signalling by the lizard *Anolis carolinensis*, with intersexual comparisons across contexts. *Behaviour*, 140: 603–634
- Otoni E. B. 2000. EthoLog 2.2: A tool for the transcription and timing of behavior observation sessions. *Behav Res Methods, Instrum, Comput*, 32: 446–449
- Pandav B. N., Shanbhag B. A., Saidapur S. K. 2007. Ethogram of courtship and mating behaviour of garden lizard, *Calotes versicolor*. *Curr Sci*, 93: 1164–1167
- Perry G., Levering K., Girard I., Garland T. 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. *Anim Behav*, 67: 37–47
- Qi Y., Wan H. F., Gu H. J., Wang Y. Z. 2010. Do displays and badges function in establishing the social structure of male toad-headed lizards, *Phrynocephalus vlangalii*? *J Ethol*, 29: 381–387
- Shine R., Langkilde T., Wall M., Mason R. T. 2005. Alternative male mating tactics in garter snakes, *Thamnophis sirtalis parietalis*. *Anim Behav*, 70: 387–396
- Torr G., Shine R. 1994. An ethogram for the small scincid lizard *Lampropholis guichenoti*. *Amphibia-Reptilia*, 15: 21–34
- Wu P. F., Wang Y. Z., Wang S. G., Zeng T., Guo H. Y., Cai H. X., Zeng Z. Y. 2002. The age structure and sex ratio of *Phrynocephalus vlangalii* (Sauria: Agamidae). *J Sichuan Univ (Nat Sci)*, 39: 1134–1139 (In Chinese)
- Xiao J. Q., Wang D. 2005. Construction of ethogram of the captive yangtze finless porpoises, *Neophocaena phocaenoides*. *Acta Hydrobiol Sin*, 29: 253–258 (In Chinese)
- Zeng Z. G., Song Y. L., Li S. Y., Zhang H., Long B., Wu Q. 2001. Roaring behavior of Hainan Eld's deer (*Cervus eldi hainanus*) male during the rut and its significance in reproduction. *Acta Zool Sin*, 47: 481–487 (In Chinese)
- Zhao K. T. 1999. *Phrynocephalus* kaup. In Zhao E. M., Zhao K. T., Zhou K. Y. (Eds.) *Fauna Sinica, Reptilia*. Beijing: Science Press, 153–193 (In Chinese)